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Matching beef cattle breeds to the environment for desired outcomes in a changing climate: A systematic review

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ABSTRACT

Cattle graze approximately 30% of global land, making their interactions with Earth's social and ecological systems of critical importance. Cattle have experienced a long process of evolution and domestication. Certain breeds are more adapted to specific environments, differentially affecting those breeds' impact on the environment, their interaction with ecosystems experiencing climate change impacts, and their capacity to provide goods and landscape management services. Emerging evidence suggests that, compared to more artificially selected conventional breeds, some less specialized, or 'heritage' beef cattle breeds exhibit unique foraging behaviors that could support desired outcomes such as biodiversity or climate change adaptation. We provide a novel, systematic characterization of breed-based behavioral differences to assist researchers and beef producers in selecting breed-based management strategies for achieving adaptation goals. We conducted a systematic search of studies that compared beef cattle breeds for behavioral trends, and found 54 studies conducted between 1966 and present day, located in 9 of the 14 major terrestrial world biomes, with 60 beef or dual-purpose breeds represented. We created a typology of the studies with respect to decade, continent, breed provenance (Continental, Criollo, Hybrid, *B. indicus*, Mediterranean, Sanga, British Isles), breed selection intensity (heritage, conventional, hybrid), biome, study intent, and whether breeds met desired outcomes described by the study authors. Most studies (69%) were conducted in arid rangeland settings in developed nations where researchers sought to minimize the environmental impacts of beef production. In comparisons of grazing behavior of heritage versus conventional types ($n = 25$ studies), and hybrid versus conventional types ($n = 18$ studies), heritage and hybrid displayed more adapted traits (e.g., better grazing distribution) in 88% and 78% of the studies, respectively. No differences were found in grazing behaviors among most studies wherein heritage breeds were compared to other heritage breeds or conventional with conventional ($n = 6$ and 15 studies, respectively). In the subset of studies coded with the intent of "foraging behavior," heritage types traveled faster across a range of pasture sizes, suggesting a lighter environmental footprint and adaptive capacity to heat impacts. Overall, our review suggests that locally derived breeds display grazing behaviors that demonstrate adaptation to their respective native environments and may help producers meet production goals in similar environments. We conclude that breeds with more natural selection tend to exhibit less rigid grazing behaviors, which is a necessary coping strategy in variable climates and locales with heterogeneous forage availability, both of which are increasingly common scenarios caused by climate change.

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1. Introduction

An estimated 1.5 billion cattle are supported worldwide (FAO, 2022). At least one third reside on grazing lands, which span 25–30% of the earth's ice-free terrestrial surface (Herrero et al., 2013; Wolf et al., 2021). Owing to their multitude of uses – draft, meat, hide, tallow, sinew, fertilizer, milk, and blood – cattle and other bovines (e.g., Yaks, Bison, Buffalo, Wisent, Guar, etc.) possess cultural significance for societies on every continent except Antarctica (Clutton-Brock, 1989). Because cattle can convert cellulose into protein useable by humans (Clutton-Brock, 1989; Felius et al., 2014) and can be managed to shape landscapes per human direction (Bailey, 2004), they perform critical roles in grazing land management. Indeed, in much of the world where cattle have co-evolved with wildlife – and even in places where they did not (e.g., North America) – cattle are important ecosystem modifiers that contribute to nutrient cycling by either selecting or avoiding particular plant species (Hobbs, 1996; Launchbaugh and Howery, 2005). However, the heterogeneous composition of grazing landscapes and the complex and variable foraging behaviors of ungulates have hindered a consensus regarding best practices for maintaining or improving grazing lands and cattle breeds that, as a result, has threatened valuable ecological and cultural resources (Briske et al., 2011). The complex socio-ecological nature of beef cattle production, the vulnerability of the landscapes that cattle and their herders inhabit, and the growing global demand for increased beef production (Xu et al., 2021) collectively merit a closer examination of the diverse grazing behaviors among different cattle breeds/types in relation to various landscapes and impending climate change threats.

The effects of climate change are already negatively impacting both livestock producers and the welfare of their animals. Major climate-related stressors on livestock and producers are arising from changes in plant community productivity[1]; heat exhaustion (or intolerance; Mader, 2014); hoof rot (in excessively muddy conditions); and increased metabolic demands (e.g., increased water requirements due to excessive panting, less grazing time due to shade seeking, etc.; Silanikove, 2000). Notably, a recent heatwave in western Kansas, USA killed over 2,000 cattle that were exposed to a week of temperatures exceeding 40°C and a humidity index <24% (Chappell, 2022). Moreover, climate change will negatively affect crops grown for livestock, even in areas where rainfall is expected to be greater than historical averages (Rötter and van de Geijn, 1999). Animal carrying capacity will reduce *or* increase as a result of drying, wetting, and warming effects depending on specific local conditions and interactions with temperatures (McIntosh et al., 2019; Rötter and van de Geijn, 1999). Declining forage nutrient quality has also been linked to climate change and may continue to deteriorate as atmospheric CO_2 levels rise (Augustine et al., 2018; Craine et al., 2017). In addition to these direct effects, climate trends are also projected to create conditions that will promote pest populations, invasive and non-native plant populations (e.g., Williamson et al., 2020). Further, climate trends may cause an increase in both number and severity of natural disasters such as tornados, hurricanes, tsunamis, wildfires, and droughts, which will amplify any or all of these scenarios, and result in more variable environmental conditions and less stable beef production systems (Rötter and van de Geijn, 1999).

The four primary tools of grazing management entail proper selection of the 1) type of animal, 2) number of animals, 3) distribution of grazing, and 4) season of use (Vallentine, 2000). Foraging behavior of grazing livestock is noteworthy because it is interconnected with the first three; any given type(s) of animal chosen (e.g., species, breed, physiological state, or age) will have a distinct distribution pattern, and will affect the number of animals that can sustainably use that landscape. The ways in which ungulates interact with and affect the grazing environment are critically necessary, but our understanding of such processes and – importantly – our ability to change them are still not fully understood (Swain et al., 2011). Several techniques are commonly used to spatiotemporally manipulate foraging behaviors (e.g., fencing, herding, and behavioral conditioning), but many of those strategies are expensive and difficult to implement (Nyamuryekung'e et al., 2022 *and sources therein*). An emerging management strategy that bypasses more cost- and labor-prohibitive approaches is selection of livestock species, breeds, or individuals that display desirable foraging patterns as a result of adapting to their surroundings (Nyamuryekung'e et al., 2022). Over the past two decades, researchers have posited that using heritage livestock species, which tend to be better matched to particular environments, could simultaneously support livestock production, ecological, and economic goals in pastoral systems of the world (Dumont et al., 2007; Holechek et al., 2020; Rook et al., 2004; Scasta et al., 2016; Spiegal et al., 2020), and support adaptive capacity, "the ability of systems, institutions, humans and other organisms to adjust to potential damage, to take advantage of opportunities, or to respond to consequences" (Spiegal et al., *this issue*; Matthews, 2018).

In a seminal review, Rook et al. (2004) explain that, when combined, animal physiology, morphology, allometry, sex, age, and behavior affect the ways in which livestock interact with and alter their environments. Dietary choices, for instance, are influenced by body size and breed, both of which present unique energy requirements and gut capacities. Supporting past work by Tolhurst and Oates (2001), they relay that "underlying differences in grazing behavior between breeds have received relatively little attention," and reference the scarcity of research on the subject at the time of publication, citing "only a small number of direct breed comparisons under controlled conditions" (Rook et al., 2004 p. 142). Global interest has expanded since, and an abundance of studies now report breed-specific variation in grazing behavior – these are the subject of this review.

Although the subject has gained appreciation over the last two decades, no documented effort has been made to characterize whether heritage cattle exhibit desirable behavioral trends across geographic gradients or how differences in genetic/geographic background may influence various levels of grazing adaptation. Endeavoring to synthesize the available research, we reviewed peer-reviewed studies that evaluated behavioral comparisons among beef cattle breeds (we refer to biotypes, hybrids, or crossbreds as 'breeds'). After providing a brief background of cattle evolution and domestication (Box 1), we describe our web search and coding methods. We then present a typology of the studies with respect to decade of publication, continental location, breed provenance and selection intensity, biome location, study intent, and whether or not the breeds studied supported outcomes hypothesized by the authors of those publications. In the subset of studies coded with the intent of 'foraging behavior,' we explored the empirical relationship between pasture size and daily distance traveled. Finally, we synthesize our findings to discuss how cattle breeds with heritage/traditional/adapted/native/indigenous genetics can serve as a resource for adaptation to current and projected climate change effects, particularly on the most marginal landscapes.

2. Materials and methods

We systematically categorized studies that describe behavior trends by beef and dual-purpose cattle type in grazingland settings, to assess whether foraging behaviors imply improved adaptation to regional ecosystems and projected climate change effects.

2.1. Web search and article retention

We conducted a systematic search of the Web of Science and Google Scholar using the English and Spanish search phrase "beef breed

[1] Changes in plant community productivity includes: changes in available feed (Klemm et al., 2020), forage loss (Estell et al., 2012); changes in forage species composition (Derner et al., 2005); and changes to landscape attributes (as in a denser woody plant layer).

Box 1
Cattle evolution and domestication in brief

Aurochs (*Bos primigenius* [Bojanus]), ancestors of modern cattle, are believed to have inhabited much of the Eurasian and African continents (Verdugo et al., 2019) in approximately 1.5–2 million years BCE, after evolving from *Bos acutifrons* (Lydekker), the oldest known progenitor of the genus *Bos* (Vuure, 2005). Archeological and genetic evidence suggests that modern cattle (*Bos taurus* [Linnaeus] and *Bos indicus* [Linnaeus]) genetically diverged from the Aurochs around 23,000 BCE (Pitt et al., 2019b). The regional adaptation of Aurochs within Eurasia and Africa is a major driving factor of regional diversity among contemporary cattle (Verdugo et al., 2019).

Genetic research points to two primary domestication events in the cattle that diverged genetically from Aurochs during the Neolithic Agricultural Revolution: one in the Fertile Crescent around 12,800–12,300 BCE, and the other in the Indus Valley around 10,300 BCE (Felius et al., 2014). Owing to their geographical distance, these events influenced the development of two groups of modern cattle (*Bos taurus* and *Bos indicus*), which are both geographically and genotypically independent from one another. Despite the homogenizing effects of modern production systems, successive generations of contemporary cattle have maintained rustic/heritage traits linked back to the Neolithic and generational learning (Provenza, 2008) resulting in natural adaptations to their localized eco-climato-geographic regimes (Wiener, 2014). Verdugo et al. (2019) recently discovered a human mediated *B. indicus* admixture/introgression in *B. taurus* cattle in the Near East around 2050 BCE that occurred in congruence with a multi-century drought, which had grave consequences for both the Mesopotamian and Egyptian empires. This reveals two important concepts: 1) extant (contemporary) cattle have evolved regional adaptations over millennia, and 2) humans have likely recognized and exploited such adaptations via selective breeding, in an attempt to combat climate changes, for at least 4000 years.

Between the time of cattle domestication and the early Industrial Revolution (1700s), cattle were kept locally and served several non-specialized purposes, including draft work and milk production, and, to a lesser degree, the production of leather, tallow, and meat (Felius et al., 2014). It was during the Industrial Revolution that the use of herd books developed, describing specially adapted cattle breeding practices, and formalizing the notion of 'breeds' (Felius et al., 2014). The advent of single purpose breeds (e.g., meat, dairy, or draft) coincided with other innovations such as improved transportation and refrigeration systems, and industrialized crop production, synergistically propelling large increases of provisioning goods throughout Europe and ultimately the world. These advancements may have come at a cost, however, as highly productive beef and dairy breeds require greater nutrient demands and are not always suited to eco-climato-geographic conditions that humans ask them to perform in (Cibils et al., 2022; Hoffmann, 2010). Demand for specialized commercial breeds has also led to a reduction of the genetic pool of *B. taurus* and *B. indicus* cattle, particularly in developed nations (FAO, 2007; Felius et al., 2014). A 2007 UN Food and Agriculture Organization report relayed that over 70% of heritage cattle are found in developing nations, and their populations are at risk of decline due to market pressures to import or crossbreed conventional breeds with heritage types (FAO, 2007). Such influences of local to global beef markets may have led to our current state of knowledge, in which a multitude of studies have examined genetic, production, and nutrition aspects of heritage, local, traditional, hybrid, and commercial cattle breeds in differing systems. Still, surprisingly few studies have evaluated the role of differing breeds in affecting either the environment in which they graze, or their adaptation to it.

behavior comparison" ("comparación de comportamiento de raza de carne") to identify candidate studies. Included in these searches were both American and British spellings ('behavior' and 'behaviour,' respectively). Articles were retained for further consideration based on an initial screening of titles and abstracts for the following criteria: a) a comparison of cattle foraging behavior, b) in a grazing land setting, and c) among two or more breeds in which d) those breeds were intended for beef or dual-purpose production. Dual-purpose breeds are those used for beef in addition to other production practices (e.g., draft, dairy, etc.). Only peer reviewed manuscripts or theses/dissertations published by a university were retained.

Our initial search returned 171,000 candidates from Google Scholar and 581 from the Web of Science. Sixty-six met most criteria, and twelve were omitted from consideration because they a) compared beef cattle with other species including river buffalo, bison, yak, or horses; b) did not compare behaviors among breeds (e.g., evaluated behavior within the same breed); or c) compared two or more breeds of dairy cows. Ultimately, we identified 54 studies for further evaluation.

2.2. Coding

2.2.1. Decade

The range of decades spanned 1960–2022. A study was assigned to a decade if it was published between the start (e.g., January 1960) and end (e.g., December 1969) of that decade.

2.2.2. Geographic location

We used Google Maps to georeference the geographic location of studies. We used ArcGIS 10 (Environmental Systems Research Institute, 2011) to map the respective number of studies per study site in the spatial context of the fourteen major terrestrial world biomes, which were developed for global scale conservation planning (Olson et al., 2001, Fig. 1). ArcGIS 10 was used (Environmental Systems Research Institute, 2011) to merge study sites within their respective biome. Likewise, cattle type was tallied per study site biome using the spatial join output from ArcGIS 10 (Environmental Systems Research Institute, 2011).

2.2.3. Breed provenance

Cattle in the studies were coded into seven provenance groups based on their geographic lineage and well-described regional and genetic characterizations (Ginja et al., 2019; Pitt et al., 2019a): **Continental** (European *B. taurus*), **Criollo** (American *B. taurus*), **Hybrid** (*B. taurus* × *B. indicus*), ***B. indicus*** (Indian sub-continent), **Mediterranean** (Any country bordering the Mediterranean; *B. Taurus*; with exceptions in France and Italy, where breeds were classified as 'Continental' and 'Mediterranean'), **Sanga** (south eastern African; stabilized *B. indicus* × *B. Taurus* [sometimes *taurindicus*]), and **British Isles** ("British"; constituting Ireland and the United Kingdom of Great Britain and Northern Ireland *B. taurus*). Crossbreds of cattle from British and Continental backgrounds (e.g., Simmental × Hereford) were lumped into the 'British Isles' group, because this pairing is typically aimed at maintaining marbling and carcass traits of British breeds and increasing offspring size and weight gains due to hybrid vigor and larger body frames of continental breeds. In instances where Criollo were crossbred with Hybrid or *indicus* cattle, they were considered Hybrids because of the resulting *B. taurus* × *B. indicus* cross. Continental French and Italian breeds were deemed such because of their derivation from non-Mediterranean biomes; for instance, Charolais cattle are from Charolais, France, which is in the eastern central region of the country within the continental temperate biome. Similarly, Piedmontese cattle are from the Piedmont region of northwest Italy, which is roughly 300 km southeast of

Fig. 1. Research sites, study counts, cattle breed provenance, selection intensity, and major study findings per major world biomes.

Charolais, in a similar continental temperate/montane biome.

2.2.4. *Breed selection intensity*

Although we did not search specifically for studies about the comparative performance of cattle that have undergone minimal selection versus those that have undergone maximal selection, many of the studies compared between the two. The articles referred to the less-selected types in many different ways, including 'heritage,' 'adapted,' 'traditional,' 'biological type,' 'indigenous,' 'low-productive,' 'native,' 'tropical,' and 'type'. Most commonly, terms like 'heritage,' 'traditional,' or 'indigenous' were used to describe older breeds with lengthy periods of adaptation to a locale and which have been developed with little human intervention (e.g., no selective breeding). 'Tropical' was commonly used to refer to *indicus* cattle. Other terms like 'high' vs 'low' productivity were used to describe breeds requiring different inputs to reach their production potentials.

We used a freeware word cloud generator (https://www.wordclouds.com/) to model the relative use of different terms used to describe backgrounds of cattle with minimal selection (Fig. 2). This method was useful for identifying and visually representing the relative use of each word in relation to one another while displaying all words simultaneously. The most common term from the word cloud was 'heritage.' Accordingly, we built a typology of cattle with three selection intensity groups: 1) **heritage**, breeds which have undergone little artificial selection and which have a long history in a specific locale; 2) **conventional**, breeds which have received a lot of artificial selection, and which have been disseminated for global beef production; and 3) **hybrid**, breeds composed of a conventional (*B. taurus*) × heritage (*B.*

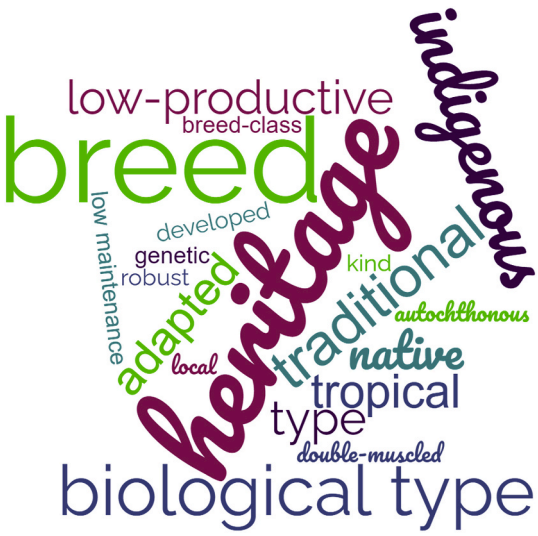

Fig. 2. Hierarchal word cloud of descriptors used to delineate heritage cattle background.

indicus) cross, which have received intermediate selection intensity. Hybrid cattle are typically composed of a highly selected British breed (e.g., Angus) and a less selected heritage breed (e.g., Brahman), and have received less than 100 years of selection by humans (e.g., Brangus cattle are composed of 5/8 Angus and 3/8 Brahman and were developed in Louisiana, USA in ~1935 with intent to combine rustic heat-adaptation traits of Brahman cattle with fast growing carcass traits of Angus cattle). Note, 'hybrid' is used as a label in both the breed provenance and breed selection intensity groupings.

2.2.5. Biological sex

Cattle biological sex was coded into five main categories. Cattle were classified as 'cows' if they were mature females who had given birth at least twice; physiological state (e.g., lactating vs dry) was not coded among cows. Cattle were classified as 'bulls' if they were intact males, regardless of age. Cattle were classified as 'heifers' if they were less than three years old and had one or fewer calves. Cattle were classified as 'steers' if they were neutered males. Cattle were classified as 'lactating/with calves' if they were nursing calves and if the mother-offspring relationship was of primary importance to the study.

2.2.6. Research intent

Research studies were coded into six intent categories based on their primary aims and methods employed: 'foraging behavior,' 'impacts on vegetation,' 'slope/distance,' 'vegetation impact on animals,' 'bite rate,' and 'diet.' Designations were determined based on the primary objectives and metrics used in each study. For instance, studies designated as, 'foraging behavior' tended to evaluate metrics like time spent resting, traveling, and grazing, time allocated to certain ecological states, distance traveled, area explored, or other patterns associated with an animal's daily activity budgets. Studies designated as 'impacts on vegetation' emphasized vegetation measurement variables to evaluate the effects of grazing by different breeds on vegetation composition and biodiversity. Studies classified as 'slope/distance' primarily evaluated breed differences in horizontal and vertical distance to a pasture-watering source and their selection or avoidance of steep versus gentle slopes. The studies deemed as 'vegetation impact on animals' sought to identify how plant physical and chemical traits might drive selection by different breeds. 'Bite rate' studies primarily quantified the sum of bites per vegetation type to compare selection by different breeds. Finally, 'diet' studies primarily evaluated diet selection via fecal samples to evaluate vegetation selection between breed types.

2.2.7. Author-described outcomes

Study results were also tallied by author-described outcomes (i.e., if authors prescribed breed-based grazing behaviors as having beneficial or non-beneficial effects on the environment), with a focus on outcome by breed selection intensity. Author-described breed-based outcomes were coded as 'different' or 'not different; ' and in instances in which differences occurred, a 'positive behavioral change' was attributed to one or more breed per study conclusions. We used this tally to summarize behavioral trends per biome.

2.3. Foraging behavior

In 24 of the 26 studies coded as 'foraging behavior' intent, we explored the empirical relationship between pasture size and daily distance traveled. To evaluate behaviors among breed type we identified six of the 24 studies that measured time spent moving (the sum of time spent traveling and grazing) and total distance traveled over 24-h periods. We calculated daily speed ($km*h^{-1}$) as a function of the distance traveled in 24 h divided by the time spent traveling.

$$(s)speed = (d)24\ h\ distance\ travled\ (km) \div (t)\ time\ spent\ traveling\ (hours).$$

Formula 1. Daily speed equation.

We reasoned that daily cattle speed would be a rational comparative measure to evaluate animal movement across studies, because it standardized (e.g., accounted for autocorrelation) the time spent traveling and distance traveled variables, which would likely have been constrained across studies due to pasture size limitations. Daily speed was calculated only for the summer growing season (summer months ranged from June–September and all studies included were in the northern hemisphere) of each of the six studies, which was assumed to represent the period of peak green forage production. We also selected speed, because Laca (1998) suggested that "encounter rate of food locations can be enhanced by concentration of search efforts in areas where food locations are more abundant, avoidance of areas already depleted, and faster search speeds" (p. 376). In other words, animals can enhance their success of encountering high quality feeds as they increase their foraging speed. Similarly, Bailey et al. (1996) reported that "there is a proportional relationship between the time large herbivores spend in a plant community and the available quantity and quality of forage," and that "foraging velocity [speed in a given direction] decreases and intake rates increases in areas of abundant palatable forage" (p. 386). This might imply that cattle reduce the length of time spent among particular plant communities as they exhibit faster speeds (ergo reducing their environmental footprint), while improving their chances of encountering better quality forages (e.g., are better suited to cope with a heterogeneous forage supply).

2.4. Synthesis of management outcomes

We developed a conceptual model to illustrate the capacity of certain breed types to meet adaptation goals, as indicated by the reviewed articles (Fig. 5). On the Y-axis, 'Environment,' was coded into two sliding scale metrics that include climate variability (from minimum to maximum; e.g., the degree to which annual climate fluctuates in relation to the long-term mean), and forage quality and quantity (high to low; e.g., the relative degree of available nutrients and number of edible plants). 'Animal,' was coded into three sliding scale metrics that include degree of genetic selection (from artificial to natural; e.g., the degree to which humans have mediated genetic flows), foraging behavior (from rigid to plastic; e.g., the degree of stochasticity in animal grazing patterns), and body size/maintenance requirements (large vs small).

3. Results

3.1. Geographic location

Most studies were conducted in North America (30), followed by Europe (14), Africa (3), Asia (3), South America (3), and Oceania (1) (Fig. 1). Studies were conducted in nine of fourteen major world terrestrial biomes, with 1 occurring in Boreal Forest/Taiga; 19 in Desert/Xeric Shrublands; 5 in Mediterranean Forests, Woodlands, and Scrub; 14 in Temperate Broadleaf and Mixed Forests; 4 in Temperate Conifer Forests; 6 in Temperate Grasslands, Savannas and Shrublands; 3 in Tropical and Subtropical Grasslands, Savannas, and Shrublands; 2 in Tropical and Subtropical Dry Broadleaf Forests; and 1 in Tropical and Subtropical Moist Broadleaf Forests ($n = 55$; this is one more than the total number of studies identified because Duni et al. [*this issue*] spans two biomes).

3.2. Research intent

Thirty-four studies intended to evaluate foraging behavior, 3 to study impacts on vegetation, 2 to study slope/distance, 2 to study vegetation impact on animals, 3 to study bite rate, and 10 to study diet (not shown in figures or tables). The number of studies evaluating grazing beef cattle behavior have increased in recent decades (Fig. 3). Only two studies matched our search criteria in the 1960s, followed by four in the 1970s, and one in the 1980s; the 1990s, 2000s, 2010s, and even 2020s have garnered 9, 16, 12, and 10 studies respectively (Fig. 3).

3.3. Biological sex

Taking biological sex into account, most studies (37) evaluated grazing behavior of cows (which did not necessarily consider certain physiological states), whereas 7 evaluated steer behavior, 5 evaluated heifer behavior, 3 evaluated steer and heifer behavior, 1 evaluated cow and calf interactions and grazing behavior, and 1 evaluated bull grazing behavior (Table 1).

3.4. Provenance group

At least 60 breeds appeared in the 54 behavioral studies, which we generalized into 7 provenance groups (Fig. 1, Table 1).

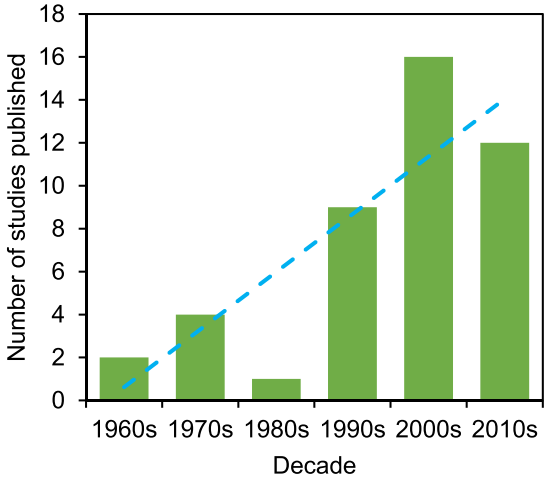

Fig. 3. Number of beef cattle breed comparison studies published per decade, 1960's - 2010's.

3.5. Speed among provenance group

Among the 24 of the 26 studies coded as 'foraging behavior' intent, daily distance (y) regressed against pasture size (x), revealed an R^2 of 0.71, suggesting that animals tended to walk farther as pasture size increased, which is expected (Fig. 4a). Across the six studies compared for traveling speed, Criollo cattle appeared to move faster than hybrid, Mediterranean, British Isle, and Continental breed groups, whereas Hybrid and Mediterranean moved at speeds similar to British breeds, but faster than Continental breeds and slower than Criollo. British Isle breeds had the most variable traveling speeds, which ranged from ~0.1–0.7 km*h^{-1}, which coincided with all the other breed groups, but was still generally slower than Criollo breeds (Fig. 4b). Still, hybrids, Mediterranean, and Continental breeds only appeared once or twice each, so their values are only an indication of expected speed differences.

3.6. Synthesis of management outcomes

Speed among provenance group (Fig. 4) aligned with our tallies of author-reported performance differences among provenance and selection intensities (Table 1, Table 2). In the 25 of 54 studies that evaluated cattle of heritage versus conventional provenance, 22 reported positive behavioral traits attributed to the heritage breed, whereas three reported no behavior difference. Another 18 of 54 studies evaluated hybrid (*indicus* × *taurus*) cattle versus conventional breeds, and 14 of those studies reported positive behavioral mechanisms attributed to hybrid types versus four which reported no behavioral differences between the breeds. Eleven of 54 studies evaluated heritage Criollo cattle or those of Spanish origin, and 10 of those studies reported positive behavioral mechanisms attributed to heritage Criollo or Spanish cows, whereas 1 showed no behavior differences between them and conventional types. Six of 54 studies evaluated heritage versus hybrid and or heritage × hybrid behavior; 3 of those studies attributed favorable behaviors to heritage breeds, whereas 2 reported no breed behavior differences. Five of 54 studies evaluated heritage breeds versus other heritage breeds, and only 3 of those reported a positive behavioral mechanism attributed to one of the heritage types, whereas the other 2 showed no behavioral differences. There were no reports of conventional breed types exhibiting favorable behavioral mechanisms compared to other non-conventional (e.g., heritage, hybrid, Criollo, etc.) types. In studies where conventional types were only compared to other conventional types (15), conclusions were much less clear; in 6 of those accounts, the authors reported favorable behavioral traits to one of the conventional types evaluated, but no differences were detected in 9 of those studies.

Among biomes, breeds that had some genetic makeup with close geographic provenance to the province (heritage or hybrid) tended to exhibit grazing behaviors associated with more desired outcomes compared to breeds derived from other zones (Fig. 1). When evaluated in hot biomes (e.g. Deserts & Xeric Shrublands), breeds derived from hotter biomes (e.g., *indicus*, hybrid, Mediterranean, and Criollo) tended to outperform breeds derived from cooler zones (e.g., British or Continental). Breeds derived from mountainous or colder biomes (e.g., Heritage British or heritage Continental) tended to outperform breeds derived from less rugged or warmer biomes (e.g., conventional British and conventional Continental types) when evaluated in cold mountainous biomes.

Based on the synthesized results of reviewed studies, we theorize that certain animal qualities, which are associated with breed types and genetic lineages (e.g., breed selection intensity class), make different breeds more or less equipped to meet adaptation goals in certain environmental conditions. We propose that three primary drivers could explain how well an animal (breed) is suited to matching agroecosystem adaptation goals (Fig. 5). Animal drivers include a) genetic selection, the degree to which humans have (artificially) or have not (naturally)

Table 1
Studies arranged by category, author, location, cattle sex, breed, breed provenance, selection intensity, and primary grazing behavior findings.

Cat.	lead author	location	biome	Cattle sex	Breeds	Breed Provenance	Selection Intensity	Primary grazing behavior findings
bite rate	Dumont et al. (2007)	UK, Germany, France	Temperate Broadleaf & Mixed Forests	steers	Devon Charolais × Friesian	British Continental	Heritage Conventional	Heritage breed at UK site selected forbs more often than conventional; Heritage breeds at other sites were less selective than conventional types
	Orr et al. (2014)	North Wyke, Devon, UK	Temperate Broadleaf & Mixed Forests	steers and heifers	North Devon Hereford × Friesian × Simmental	British British	Heritage Conventional	Heritage breed yearlings had greater total jaw movements, but spent less time ruminating compared to conventional types.
	Morris et al. (1993)	Palmerston North, New Zealand	Temperate Broadleaf & Mixed Forests	bulls	Piedmontese × Friesian	Continental	Conventional	Bite rate and grazing time of Blue Belgian x Friesian was less than Friesian; Blue Belgian × Friesian daytime idling time was greater than Piedmontese × Friesian or Friesian counterparts. Few differences between provenance groups.
diet	Berry et al. (2002)	Swiss Alps, Switzerland	Temperate Broadleaf & Mixed Forests	cows	Highland Brown Swiss	British Continental	Heritage Conventional	Heritage breed was more productive on Alpine pastures than conventional cows and better utilized pastures with poor nutrient quality
	De Alba Becerra et al. (1998)	Las Cruces, NM, USA	Deserts & Xeric Shrublands	cows	Beefmaster Brangus Barzona	Hybrid Hybrid Hybrid	Hybrid Hybrid Hybrid	No diet composition differences determined.
	Estell et al. (2022)	Las Cruces, NM	Deserts & Xeric Shrublands	cows	Raramuri Criollo Angus	Criollo British	Heritage Conventional	Heritage breed consumed less black grama (critical forage resource) than conventional.
	Forbes (2005)	Southeast Texas, USA	Temperate Conifer Forests	cows	Angus × Brahman Angus	Hybrid British	Hybrid Conventional	Conventional spent more time seeking shade than hybrid; but no differences in grazing times or diet were detected.
	Forbes (2005); Forbes et al., (1998)	West Texas, USA	Deserts & Xeric Shrublands	cows	Tuli × Brahman Angus Brahman Angus × Brahman	Hybrid British *Indicus* Hybrid	Hybrid Conventional Heritage Hybrid	Conventional grazed for least time, but exhibited longer residence times and slower passage rates than *Indicus* hybrid counterparts.
	Marquardt et al. (2018)	Gran Chaco, Argentina	Tropical & Subtropical Dry Broadleaf Forests	cows	Criollo Chaqueño Brahman × Criollo Chaqueño	Criollo Hybrid	Heritage Hybrid	Heritage breed tended to eat more woody plants and gained weight in the intermediate dry-rainy season compared to hybrids.
	Winder et al. (2000)	Las Cruces, NM, USA	Deserts & Xeric Shrublands	cows	Barzona Brangus Beefmaster	Hybrid Hybrid Hybrid	Hybrid Hybrid Hybrid	No diet composition differences determined.
	Winder et al. (1996)	Las Cruces, NM, USA	Deserts & Xeric Shrublands	cows	Brangus Hereford Angus	Hybrid British British	Hybrid Conventional Conventional	Compared with conventional, hybrid had greater preference for dropseed sand consumed more Yucca and total shrubs.
	Sprinkle (1992)	Montana, USA	Temperate Grasslands, Savannas & Shrublands	cows	Tarentaise Hereford Hereford × Tarentaise	Continental British British	Heritage Conventional Conventional	Hereford and Herford × Tarentaise decreased fecal output as body condition increased during lactation, whereas Tarentaise fecal output did not change.
	Quezada (1998)	Las Cruces, NM, USA	Deserts & Xeric Shrublands	cows	Barzona Beefmaster Brangus	Hybrid Hybrid Hybrid	Hybrid Hybrid Hybrid	Barzona selected least NDF and greatest digestibility diet compared to (*indicus* × *taurus*) counterparts
Foraging behavior	Aharoni et al. (2014)	Galilee, Israel	Mediterranean Forests, Woodlands & Scrub	cows	Baladi Beefmaster × Simford	Mediterranean Hybrid	Heritage Hybrid	Heritage was more active in all seasons, walked farther distances, spent more time grazing, and were more metabolically efficient in low quality herbage conditions than hybrids.
	Aharoni et al. (2009)	Galilee, Israel	Mediterranean Forests, Woodlands & Scrub	cows	Baladi Beefmaster × Simford	Mediterranean Hybrid	Heritage Hybrid	Heritage cows grazed more, walked more, had more feed intake per unit metabolic bodyweight, and had lower locomotion costs than hybrid counterparts.
	Braghieri et al. (2011)	Basilicata, Italy	Mediterranean Forests, Woodlands & Scrub	cows	Podolian Chianina Romagnola	Mediterranean Mediterranean Mediterranean	Heritage Heritage Heritage	No differences in activity budgets detected, but Chianina selected more forbs than breed counterparts, Podolian cows selected more ferns than breed counterparts.
	De Souza Gomes (1983) D'Hour et al. (1994)	Santa Rita, AZ, USA	Deserts & Xeric Shrublands	cows heifers	Barzona Hereford Salers	Hybrid British Continental	Hybrid Conventional Heritage	No differences in diet composition or behavior detected.

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Table 1 (*continued*)

Cat.	lead author	location	biome	Cattle sex	Breeds	Breed Provenance	Selection Intensity	Primary grazing behavior findings
		Massif Central, France	Temperate Broadleaf & Mixed Forests		Limousin	Continental	Conventional	Conventional heifers grazed longer than Salers (conventional, but more rustic) counterparts, but Salers had greater bite rates. Salers were less affected by decrease in available herbage vs Limousin counterparts.
	Dolev et al. (2014)	Galilee, Israel	Mediterranean Forests, Woodlands & Scrub	cows	Baladi Beefmaster × Simford	Mediterranean Hybrid	Heritage Hybrid	Heritage cows were more active across all seasons, walked farther, and grazed for longer periods than hybrids.
	Duni et al. *this issue*	California, Utah, USA	Deserts & Xeric Shrublands; Mediterranean Forests, Woodlands & Scrub	cows	Raramuri Criollo Angus	Criollo British	Heritage Conventional	Heritage cows traveled farther, spent more time grazing, and explored larger pasture areas during seasons of vegetation dormancy compared to conventional.
	Fraser et al. (2009)	Brecon, Powys, UK	Temperate Broadleaf & Mixed Forests	steers	Welsh Black Charolais crossbreds	British Continental	Heritage Conventional	No behavioral differences detected.
	Funston et al. (1991)	Montana, USA	Temperate Grasslands, Savannas & Shrublands	cows	Hereford Simmental × Hereford Angus × Hereford Simmental × Hereford (75/25) Tarentaise × Hereford Tarentaise × Simmental × Hereford Charolais × Simmental × Hereford	British British British Continental British Continental Continental	Conventional Conventional Conventional Conventional Conventional Conventional Conventional	Angus × Hereford grazed longer than Angus and Simmental × Hereford. Simmental × Hereford traveled greater distances than other breeds. Tarentaise × Simmental × Hereford exhibited more bite rates than Hereford, but no differences were determined among other breeds.
	Hammond (1993)	Central Florida, USA	Temperate Conifer Forests	heifers	Senepol Hereford	Hybrid British	Hybrid Conventional	Hybrid grazed longer and exhibited lower internal body temperatures compared to conventional.
	Herbel and Nelson (1966)	Las Cruces, NM, USA	Deserts & Xeric Shrublands	cows	Santa Gertrudis Hereford	Hybrid British	Hybrid Conventional	Hybrid cows walked farther and more often than conventional. Conventional grazed for more time than hybrid.
	Herbel et al. (1967)	Las Cruces, NM, USA	Deserts & Xeric Shrublands	cows	Santa Gertrudis Hereford	Hybrid British	Hybrid Conventional	Hybrid cows walked farther than conventional. Grazing distribution was overall similar among breeds.
	Hessle et al. (2008)	Skara, Sweden	Temperate Broadleaf & Mixed Forests	heifers	Väneko Charolais	Continental Continental	Heritage Conventional	Few breed differences determined, but heritage heifers exhibited increased activity and more diverse habitat selection than conventional.
	Herrera Conegliano et al., 2022	Gran Chaco, Argentina	Tropical & Subtropical Dry Broadleaf Forests	cows	Argentine Criollo Angus	Criollo British	Heritage Conventional	Heritage traveled and explored larger areas during dry winter months than conventional.
	Huber et al. (2008)	Mbarara district, SW Kenya	Tropical & Subtropical Moist Broadleaf Forests	heifers	Ankole Ankole × Holstein	Sanga Hybrid	Heritage Hybrid	No behavioral differences detected. Authors note Ankole (heritage) heifers exhibited greater herd cohesion than crossbred counterparts.
	Kanyenda (1979)	Kabete, Kenya	Tropical & Subtropical Grasslands, Savannas & Shrublands	cows	Boran Hereford	Sanga British	Heritage Conventional	Heritage cows spent more time walking than conventional cows. Conventional cows spent more time grazing in the wet season, but heritage spent more time grazing during the dry season.
	Kropp et al. (1973)	El Reno, OK, USA	Temperate Grasslands, Savannas & Shrublands	heifers	Hereford Hereford × Holstein Holstein	British British Continental	Conventional Conventional Conventional	Conventional grazed and idled for longer periods than other conventional breeds.
	McIntosh et al. (2021)	Las Cruces, NM, USA	Deserts & Xeric Shrublands	steers	Raramuri Criollo Criollo crossbreds	Criollo Hybrid	Heritage Hybrid	No behavior differences detected.
	Nyamuryekung'e et al. (2021)	Las Cruces, NM, USA	Deserts & Xeric Shrublands	cows	Raramuri Criollo Angus Raramuri Criollo	Criollo British Criollo	Heritage Conventional Heritage	Heritage cows had lower internal temperatures than conventional cows. Heritage also traveled farther, faster, and spent more time grazing and less time resting than conventional.

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Table 1 (*continued*)

Cat.	lead author	location	biome	Cattle sex	Breeds	Breed Provenance	Selection Intensity	Primary grazing behavior findings
	Nyamuryekung'e et al. (2020)	Las Cruces, NM, USA	Deserts & Xeric Shrublands	cows/ calves	Angus	British	Conventional	Heritage cows were spatially unconstrained by calves via exhibiting 'follower' mothering style. Conventional cows were constrained by 'hider' mother style.
	Nyamuryekung'e et al. (2022)	Las Cruces, NM, USA	Deserts & Xeric Shrublands	cows	Raramuri Criollo Angus	Criollo British	Heritage Conventional	Heritage cows exhibited less herd cohesion and greater selection for greenest patches on the landscape than conventional cows.
	Pauler et al. (2020a)	Swiss Alps	Temperate Broadleaf & Mixed Forests	cows	Braunvieh Highland Angus × Holstein	Continental British British	Conventional Heritage Conventional	Heritage cows exerted less static pressure on landscape, exhibited a more even grazing distribution, and moved farther from water and up steep slopes compared to conventional Angus x Holstein and conventional but rustic Braunvieh,
	Peinetti et al. (2011)	Las Cruces, NM, USA	Deserts & Xeric Shrublands	cows	Raramuri Criollo Angus	Criollo British	Heritage Conventional	Heritage cows foraged at greater spatial extents during dry fall periods than conventional cows
	Räisänen (2014)	Ol Pejeta Conservancy, Kenya	Tropical & Subtropical Grasslands, Savannas & Shrublands	cows	Ankole Boran	Sanga Hybrid	Heritage Hybrid	Heritage cows tended to spend more time resting, and more time seeking shade, and exhibited a looser herd structure than hybrid cows. Looser herd structure possibly due to horns.
	Román-Trufero et al. (2019)	Spain	Temperate Broadleaf & Mixed Forests	steers	Asturian Mountain Asturian Valley	Mediterranean Mediterranean	Heritage Heritage	Asturian Mountain (heritage breed) steers tended to graze on shrubby heathlands more often than Asturian Valley (heritage breed, but more conventionally used) steers, but both exhibited similar grazing durations.
	Russell et al. (2012)	Las Cruces, NM, USA	Deserts & Xeric Shrublands	cows	Brahman Brangus Angus	*Indicus* Hybrid British	Heritage Hybrid Conventional	Heritage cows traveled farther and in more sinuous pathways than hybrid or conventional, but no breed differences in distance to water were detected.
	Sheehy (2007)	Zumwalt prairie Oregon, USA	Temperate Grasslands, Savannas & Shrublands	cows	Angus Hereford Corriente × Longhorn	British British Criollo	Conventional Conventional Heritage	Heritage cattle traveled and rested farther from watering sources and accessed water less often than two conventional breeds in the dormant fall season.
	Sneva (1970)	Burns Oregon, USA	Deserts & Xeric Shrublands	steers	Brahman × Hereford Hereford	Hybrid British	Hybrid Conventional	Hybrid steers tended to walk farther, spend more time traveling, and less time grazing than conventional steers.
	Spiegal et al. (2019)	Las Cruces, NM	Deserts & Xeric Shrublands	cows	Raramuri Criollo Angus	Criollo British	Heritage Conventional	Heritage cows expressed larger home ranges and half as many hotspots (areas of reuse) in dry seasons compared to conventional cows.
	Sprinkle et al. (2000)	Uvalde, TX, USA	Temperate Grasslands, Savannas & Shrublands	steers	Brahman × Angus Tuli × Angus Angus	Hybrid Hybrid British	Hybrid Hybrid Conventional	Conventional steers had greater gastrointestinal tract load, accumulated more metabolic heat compared to hybrid steers. Hybrid Tuli × Angus steers spent more time seeking shade than other steer types in early summer, but spent more time in the sun than breed counterparts in late summer.
	Stricklin et al. (1976)	Pennsylvania, USA	Temperate Broadleaf & Mixed Forests	cows	Angus Angus × Charolais	British British	Conventional Conventional	Conventional Angus × Charolais spent more time grazing than conventional Angus, but few other differences detected.
	Taborda et al. (2018)	Paysandú, Uruguay	Tropical & Subtropical Grasslands, Savannas & Shrublands	cows	Bonsmara × Hereford Hereford	Hybrid British	Hybrid Conventional	Conventional cows spent more time resting and more time seeking shade than hybrid cows; Hybrid cows showed lower internal temperatures in hot summer seasons and grazed under hotter conditions.
	Tofastrud et al. (2020)	Norway	Boreal Forests/Taiga	cows	Hereford Charolais Limousin	British Continental Continental	Conventional Conventional Conventional	No differences of time spent grazing detected
impacts on vegetation	White Pas and Saxton (1998)	Baton Rouge, Louisiana, USA	Temperate Conifer Forests	steers	Hereford Hereford × Brahman	British Hybrid	Conventional Hybrid	No behavioral differences detected
	Isselstein et al. (2007)	UK, Germany, France	Temperate Broadleaf & Mixed Forests	steers and heifers	Devon Angus Salers	British British Continental	Heritage Conventional Heritage	No breed effects on vegetation detected.

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Table 1 (*continued*)

Cat.	lead author	location	biome	Cattle sex	Breeds	Breed Provenance	Selection Intensity	Primary grazing behavior findings
					Charolais × Friesian	Continental	Conventional	
					Simmental	Continental	Conventional	
					Charolais	Continental	Conventional	
	Pauler et al. (2019)	Switzerland, Germany	Temperate Broadleaf & Mixed Forests	cows	Highland	British	Heritage	Heritage cows affected a positive response on vegetation diversity (reduced woody species cover, increased epizoochoric species) compared to pastures grazed by conventional cows.
					Limousin	Continental	Conventional	
					Simmentaler	Continental	Conventional	
					Braunvieh	Continental	Conventional	
					Angus	British	Conventional	
					Charolais	Continental	Conventional	
	Scimone et al. (2007)	UK, Germany, France	Temperate Broadleaf & Mixed Forests	steers and heifers	Devon	British	Heritage	No breed effects on vegetation detected.
					Angus	British	Conventional	
					Salers	Continental	Heritage	
					Charolais × Friesian	Continental	Conventional	
					Simmental	Continental	Conventional	
					Charolais	Continental	Conventional	
slope/dist.	Bailey et al. (2001)	Havre, Montana, USA	Temperate Grasslands, Savannas & Shrublands	cows	Tarentaise	Continental	Heritage	Heritage cows and ¾ conventional Tarentaise × Hereford cows used steeper slopes in one study year and traveled to farther distances from water compared to conventional Hereford and crossbreds thereof.
					Hereford	British	Conventional	
					Tarentaise × Hereford and crossbreds thereof	British	Conventional	
	VanWagoner et al. (2006)	Havre, Montana, USA	Temperate Grasslands, Savannas & Shrublands	cows	Piedmontese	Continental	Heritage	Heritage Piedmontese-sired cows traveled farther from water and tended to utilize steeper slopes more than Conventional Angus-sired cows.
					Salers	Continental	Heritage	
					Angus	British	Conventional	
					Charolais	Continental	Conventional	
vegetation impacts on animals	Pauler et al. (2020b)	Swiss Alps	Temperate Broadleaf & Mixed Forests	cows	Braunvieh	Continental	Conventional	Plants of better forage quality were preferred among conventional cows, but less often selected by heritage cows. Hybrid cows expressed less selective grazing preferences than conventional cows resulting in more diverse pasture-level species composition.
					Highland	British	Hybrid	
					Angus x Holstein	British	Conventional	
	Duff et al. (2002)	Des Moines, NM, USA	Temperate Grasslands, Savannas & Shrublands	steers	Brangus	Hybrid	Hybrid	Hybrid consumed more toxic locoweed in study year year 1, week 1; and year 2, week 1, 2, 3 than either conventional steer type. Alkaline phosphatase levels did not differ among breed, however.
					Charolais	Continental	Conventional	
					Hereford	British	Conventional	

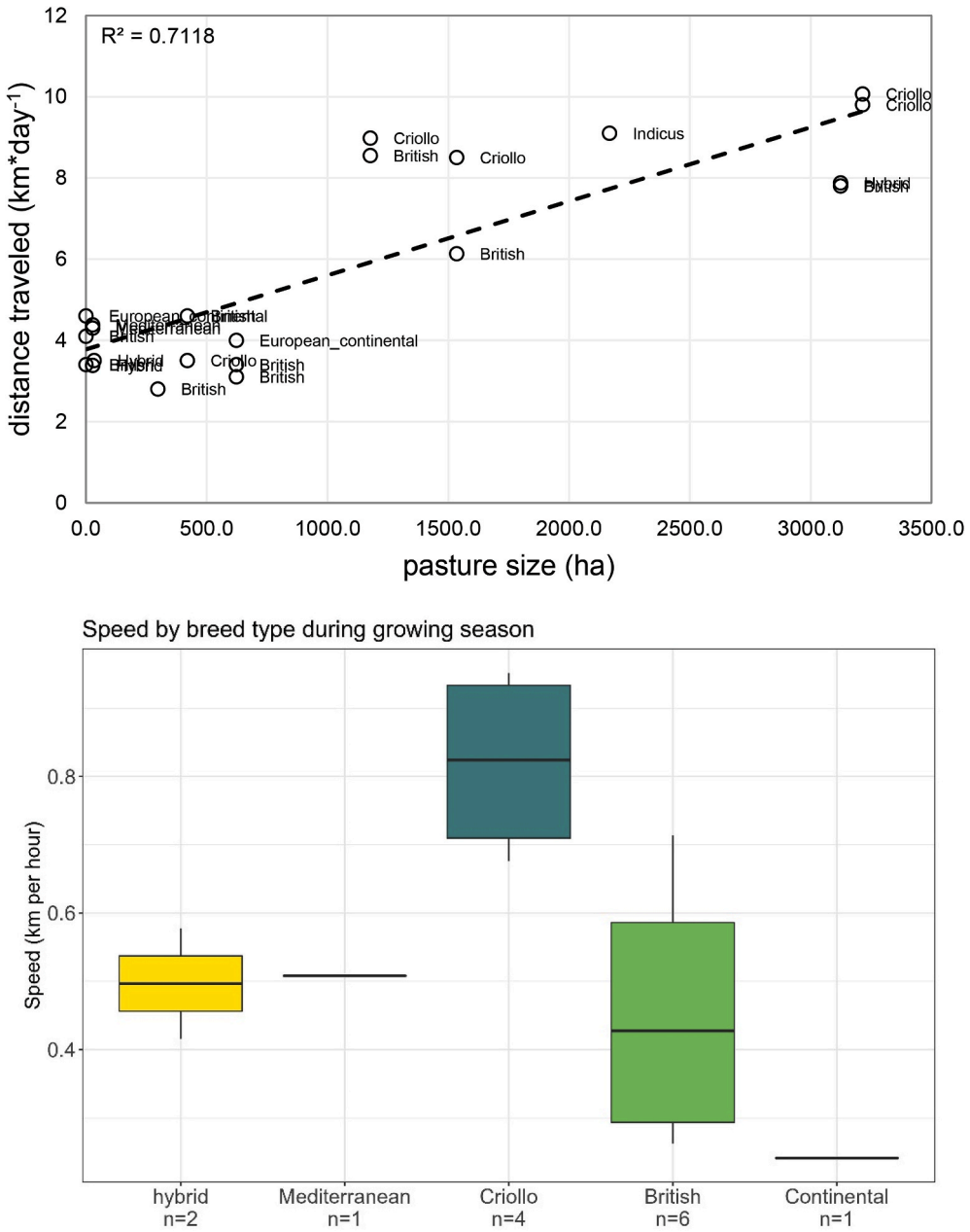

Fig. 4. a) Relationship between pasture size and distance traveled per 24-h (n = 24 studies); and b) Speed by breed type during summer growing season (n = 6 studies). Sample sizes in 4b denote number of provenance groups across studies.

influenced the genetic phylogeny of a breed type; b) foraging behavior, the ability of an animal to adjust its grazing patterns to cope with environmental conditions (e.g., from more ridged [less ability to adjust] to more plastic [more ability to adjust]); and c) body size and maintenance requirements, the morpho-physiological constraints that dictate how much and of which quality feed an animal must consume (large body size and/or large maintenance requirements vs small body size and/or less maintenance requirements). We propose two primary environmental drivers that affect how well an animal type or breed will be matched to adaption goals. These include a) climate variability, the degree to which local weather fluctuates from year-to-year (from minimal [e.g., a predictable climate pattern] to maximum [e.g., an unpredictable climate pattern]); and b) forage quality and quantity, the nutritive value and relative amount of forage available to an animal (from high amounts [of quantity and/or quality] to low). The architecture of the model (Fig. 5) was informed by Allred et al. (2011) who conceptualized the conservation value of grazing animals in response to environmental and animal complexities.

4. Discussion

4.1. Research history & location

Our synthesis revealed that studies of beef cattle breed behaviors have multiplied over the past few decades, which we contend has been in response to emerging trends, including climate change, improved technology, and widespread interest in more sustainable livestock production. Considering global beef demand and production has increased from the 1960s through the present (Smith et al., 2018) and climate change factors like global ambient temperature are affecting business-as-usual beef production systems, we regard this research as timely and much needed. We speculate that the majority of studies

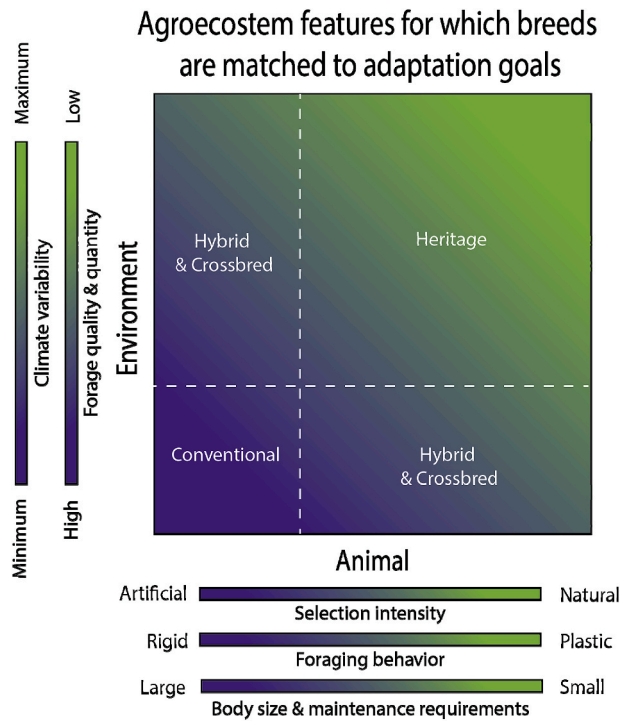

Fig. 5. Theoretical metrics of adaptation of beef cattle breeds (animal) in relation to agroecosystem environment.

conducted have occurred in either the United States (US; leading beef producing country) or the European Union (third leading beef producer), because a) most conventional breeds reside in those regions, b) they are major global beef production hubs, and c) novel management strategies such as incorporating heritage or local breeds will be necessary to combat climate changes in those locales (Holechek et al., 2020; Smith et al., 2018). Also, the presence of at least one land grant institution in each US state and investment in research from the Federal Government and fewer agricultural universities among European nations may explain why the US is a leader in this research domain. In addition, technological advancements such as access to reliable, wearable global positioning system (GPS) devices, which were used in several studies reported, have revolutionized this research domain (Bailey et al., 2018; Rivero et al., 2021).

We were unable to find beef cattle behavioral breed comparison studies from either Brazil, China, or Australia, and it would be interesting to expand research to these biomes, which are among the leading beef producing nations (Xu et al., 2021; See Appendix A for more detailed discussion.). Our search was constrained to singular phrases in only two languages (English and Spanish) thus there is a strong chance that research studies published in other languages and from other countries (e.g., Brazil) went undetected. Emerging evidence suggests that over 90% of indexed natural science manuscripts are published in English (Di Bitetti and Ferreras, 2017), therefore it is possible that ~10% of studies in the realm of our search went undetected because of language bias. It is important to note that we did not include the wealth of studies comparing heritage or hybrid vs. conventional cattle outside of the realm of behavior.

4.2. Breed representation

Some reports suggest there are over 950 cattle breeds in existence globally (Felius et al., 2015); thus, though our review was comprehensive for our study questions, it captured only ~6% of cattle breeds. We recognize that several other studies report dairy cattle breed comparisons and others report individual characterizations of breed behavior without comparison to another, but those were beyond the scope of this review. It is valuable to note that conventional cattle types were often treated as controls in reported studies likely because of their prevalence in beef supply chains; we speculate, also, that the extensive genetic and production data that has been published regarding conventional breeds has impacted their being used as controls in ethological studies (Felius et al., 2015). Heritage cattle were evaluated in 31/54 studies (57%) and hybrids in 20/54 studies (37%) which corroborates our prediction that research in this domain has gained traction as researchers and producers seek alternate and regionally adapted breeds to cope with climate and demographic changes. Additionally, the large number of studies focused on hybrid cattle breeds (*indicus* × *taurus*) may indicate a desire by producers to find locally adapted animals that meet both market and ecological demands (e.g., fast growing animals but which are heat tolerant and better suited to hot biomes).

Generally, when the same heritage breed appeared in more than one study, it was the result of a research group who aimed to evaluate different animal types of the breed such as sex (heifers versus steers) or physiological state (lactating versus non-lactating). For instance, researchers at the United States Department of Agriculture – Agricultural Research Service and New Mexico State University in New Mexico, USA were responsible for all 8 Raramuri Criollo studies used in this review. Likewise, researchers from Newe Ya'ar Research Center in Ramat Yishay, Israel conducted all 3 of the studies involving heritage Baladi cattle. This research group-centric trend of evaluating heritage breeds was less common for conventional breeds like Angus, Hereford, or Charolais, which were commonly deemed to be statistical 'control' groups by various research institutions. The large number of breed behavior studies in New Mexico have been conducted to help researchers provide options for the complicated beef production systems found in that region. Cows must wean high yielding calves on marginal rangelands of the Chihuahuan Desert to satisfy backgrounding and feedlot demands and still remain in sufficient body condition to breed annually (Spiegal et al., 2020).

Table 2
Behavioral performance comparisons of breed selection intensity classes, tallied per author described results.

Breed Selection intensity group comparison	Number of studies evaluated (*n*)	% of studies in which heritage or hybrid performance was coded as beneficial	% of studies in which conventional performance was coded as beneficial	% of studies with no difference detected
Heritage vs Conventional	25	88.0	0.0	12.0
Heritage vs Heritage	6	33.3	0.0	66.7
Heritage vs Hybrid	6	60.0	0.0	40.0
Conventional vs Hybrid	18	77.8	0.0	22.2
Conventional vs Heritage Criollo and Spanish	11	90.9	0.0	9.1
Conventional vs Conventional	15	0.0	40.0	60.0

*note that total $n > 54$, which is greater than the total number of studies reviewed because some studies compared multiple breed types against one another (e.g., heritage vs conventional vs hybrid).

4.3. Study biome

A third of studies were conducted in the Desert and Xeric Shrubland biome (19/54; ~35%), possibly because these areas are particularly prone to degradation by drought, livestock grazing and other human-mediated production practices if mismanaged, and are among the most spatiotemporally variable climate regimes. This and other rangeland biomes (e.g., temperate grasslands, Mediterranean forests, tropical grasslands, and conifer forests) were the environmental context for 69% of the studies, which also might imply that researchers in such ecoregions recognize how business as usual cattle systems in arid environments are becoming threatened and that novel strategies like incorporating heritage genetics could mediate existential climate threats (Sayre et al., 2013). These environments are examples of highly variable climates with limited forage quantity and quality, where heritage cattle might be best suited to matching adaptation goals (Fig. 5). Even still, 14 of 54 (~26%) studies were conducted in the Temperate Broadleaf and Mixed Forest ecoregion, which are equally useful considering that biome poses its own challenging dilemma as it is considered the most anthropogenically disturbed (e.g., is highly developed, severely deforested, and features large numbers of non-native plant species) owing to desirable human habitat characteristics like access to natural resources and less variable cropping systems (Hannah et al., 1995). In spite of forage abundances and more climate predictability in the Temperate Broadleaf and Mixed Forest ecoregion, cropping and urban sprawl pressures will likely force livestock grazing into more marginal ecotones within that biome, hence some combination of heritage or conventional × heritage crossbreds might meet adaptation goals, there, too (Fig. 5).

4.4. Cattle biological sex

Nearly 70% of studies evaluated cow behavior, as opposed to, for instance, heifer behavior. This trend makes sense considering it's primarily cows which are raised in extensive grazing systems, wherein they are typically bred on an annual basis and their calves are weaned and transferred into different backgrounding systems (Spiegal et al., 2020). An adult bovine is deemed a cow when she has had 2 or more calves; beef cows in the US have an average reproductive lifespan of 5–10 y (Szabó and Dákay, 2009), thus, again, the explicit attention given to their grazing behavior is justifiable. Studies evaluating steer behavior, heifer behavior, or steer and heifer behavior constituted 7, 5, and 3 studies, respectively; generally, studies evaluating steer behavior sought to evaluate breed performance in backgrounding or finishing systems, whereas those evaluating heifer behavior had similar goals as 'cow' studies, which were to characterize breed-based differences in grazing behavior in extensive grassland systems. Eight of 10 steer studies were conducted in the period since 2000, which may be a result of an increased interest in grass finished beef production. Only 1 study evaluated bull grazing behavior, and those animals were 15-months old and raised for beef in a pasture-based system, thus were effectively evaluated for the same criterion as steers in companion studies. It is worth noting that, anecdotally, evaluating bull behavior is challenging because of limited sample sizes and because they cause damage to tracking equipment (e.g., GPS). As precision GPS (or other) tracking systems increase in availability and applicability, it may become feasible to evaluate bull performance in real-time and to incorporate their grazing behavior into common genetic metrics such as expected progeny difference (EPD) models in order to selectively breed for specific behavioral traits (Bailey et al., 2015). Another challenge for evaluating differences in foraging behavior among bulls is that during the breeding season behavior is likely dominated by mating and competition among peer bulls, while during periods outside of the mating season bulls are often separated from the cow herd and smaller number of bulls in a pasture may congregate together making comparisons more difficult.

4.5. Cattle provenance speed

The regression results of foraging behavior studies strongly imply a positive relationship between pasture size and daily distance traveled, which may indicate that some breeds are better equipped to forage among different sized pastures and/or landscapes with more or less heterogeneous forage supplies. Nevertheless, these results are limited by the nature of this review and could suggest traveling distances change as a function of distance to water or some other phenomenon (e.g., topography; see Raynor et al., 2021), hence a coordinated effort among research institutions could help disentangle such findings.

Five cattle provenances were represented in the meta-analytical comparisons for traveling speed. These studies occurred in three biomes (Deserts & Xeric Shrublands, Mediterranean Forests, Woodlands, & Scrub; and Temperate Grasslands, Savannas, & Shrublands) across two continents (North America and Asia). Hybrid, Mediterranean, and Criollo tended to travel faster compared to British or Continental types. Still, British breeds (which included Hereford and Angus) exhibited the most variability in travel velocities across studies, which could be the result of the larger number of studies, but might also represent local adaptations by British animals to different ecological zones. It is common for producers to retain adapted cows even in drought conditions to avoid using less adapted animals, because of an implicit understanding of local adaptations (Bailey et al., 2010). Criollo tended to move the fastest compared to all other types, but British types sometimes traveled at comparable speeds. In the Chihuahuan Desert, Criollo often explore larger areas and travel more than British counterparts, but primarily do so in the dry season when forage is least available (Cibils et al., this issue and sources therein). During the peak green season when forage is more plentiful and higher quality, some overlap between British and Criollo speeds might be expected because cattle do not need to travel to find preferred vegetation (Cibils et al., this issue). Criollo exhibited the second-most variability in daily speed, which may be affected by a comparatively large sample size, but might also represent their ability to adjust behaviors in response to changes in the forage supply. Cibils et al. this issue evaluated behavioral plasticity, the capacity of an animal to adjust its behaviors to cope with environmental changes, of Criollo and Angus cattle across North and South America and concluded that Criollo exhibited more plastic grazing tendencies than conventional counterparts did. Still, most breed comparisons focused on daily or weekly breed averages and formal breed comparisons focused on evaluating behavioral plasticity are lacking.

4.6. Author described outcomes and drivers

A majority of studies that compared heritage cattle types with conventional types reported that heritage cattle behavior was superior for a number of traits. Heritage cattle often (>75% of the time; Table 2) exhibited more adaptable behaviors compared to conventional counterparts, such as: increased rumination time; a broader range of dietary items; a propensity for ranging farther from watering sources; selecting more diverse habitats; spending more time searching and grazing and less time resting; exhibiting less concentrated grazing patterns; increased use of steep slopes and rugged terrain; less grazing selectivity; and an increased ability to safely ingest poisonous plants (see Appendix B.1. for more detailed discussion). Most studies that compared hybrid and conventional breed types reported that hybrids exhibited more adaptation behaviors than purebred British and Continental conventional cattle (Table 2). Almost all studies that evaluated heritage Criollo cow behavior reported more extensive spatial grazing patterns compared to conventional counterparts (Table 2). These findings strongly imply that heritage beef cattle breeds behave in ways that are more sustainable than conventional types.

Most studies concluded that such desirable grazing behaviors were attributable to physiological and genetic mechanisms of heritage cattle types (Tables 1 and 2). For instance, Pauler et al. (2020a) determined

that heritage Scottish Highland cows had smaller body weights and larger hoof sizes compared to conventional types, which resulted in their exploring larger areas and exerting less kinetic force on pasture vegetation and soils (see appendix B.2. for more examples). Heat adaptation may be another mechanism that allows heritage breed types to use extensive landscapes more evenly than conventional cattle. Morphological traits like slick hair, increased surface areas (baggy skin), lighter body weights, and lighter colors might play a role in better thermotolerance and allow animals to travel faster and farther from water than less adapted breeds in hot conditions (Aharoni et al., 2009; McIntosh et al., 2020; Nyamuryekung'e et al., 2021; Russell et al., 2012). Breed selection appears less important in cases where either two or more breeds are locally adapted or cases where pasture-level vegetation is relatively uniform. For instance, in the study by Braghieri et al. (2011), researchers compared three locally adapted heritage Italian breeds, Chianina, Romagnola, and Podolian, and found minimal differences between their diel grazing behaviors even though Chianina and Romagnola have been selected for growth and productivity while Podolian received less selection pressure. Only one third of studies that compared heritage versus heritage cattle behavior found any breed-based differences (Table 2). In instances where conventional breed grazing behavior was compared against another conventional breed, 60% of authors described no foraging behavior differences (Table 2; Appendix B.3.). In more predictable pasture conditions, Stricklin et al. (1976) reported minimal differences between conventional Angus and Charolais × Angus that grazed planted pastures in Pennsylvania, USA, although crossbreds tended to graze longer than purebreds.

4.7. Desired outcomes from matching beef cattle breeds to the environment

Most studies showed that the advantage of breeds with heritage genetics or otherwise native and/or adapted attributes of their grazing locale lowered their environmental footprints (Fig. 1). For instance, heritage Scottish Highland Cattle evaluated by Pauler et al. (2019; 2020a; 2020b) explored larger areas, exerted less kinetic pressure on soils, and exhibited a wider diet breath that was associated with more biodiverse pasture-level vegetation results compared to conventional breed types of British or Continental origin. Those studies were all conducted in the Swiss Alps in the Temperate Broadleaf and Mixed Forests biomes, but on the periphery of the Boreal Forests & Taiga, which is the same biome that Scottish Highland cattle originated from in Northern Scotland. Similarly, different Criollo biotypes examined by Cibils et al. (2023 *and sources therein*), which were conducted in the Deserts & Xeric Shrublands, Mediterranean Forests, Woodlands & Scrub, Temperate Grasslands, Savannas & Shrublands, and Tropical & Subtropical Dry Broadleaf Forests all showed increased foraging plasticity, a tendency to graze farther from water with fewer concentrated grazing locations (hotspots), a capacity to be less spatially constrained by temperature or physiological state (e.g., when nursing a calf), and an ability to select more diverse diets (Fig. 1). Two recent studies, which did not appear in our literature review, also demonstrated foraging behavior advantages by Caqueteño Criollo in Colombia and Raramuri Criollo in northern Mexico, respectively (Londoño-Paéz et al., 2022; Roacho et al., *this issue*). Criollo cattle have inhabited each of those biomes for ~500 years and were sourced initially from the Mediterranean Forests, Woodlands & Scrub biome in southern Spain, thus have been acclimated to such regions for over 5 centuries (Armstrong et al., 2022). These same conclusions could be drawn for several other breed types (as expressed in Fig. 1). Importantly, breed-based grazing behavior differences seem less divergent in biomes where breeds originated from. For instance, studies evaluating heritage and conventional British types in the Temperate Broadleaf and Mixed Forests of North America and Europe revealed relatively few behavioral differences (Table 2 and Fig. 1; Dumont, B. et al., 2007; Isselstein et al., 2007; Orr et al., 2014; Scimone et al., 2007; Stricklin et al., 1976). The same could be said of heritage breeds originating from the same biomes, as in the case of Räisänen and Räisänen (2014) who compared Boran and Ankole cattle on Kenyan Tropical & Subtropical Grasslands and found relatively few differences between either locally derived breed (Table 2 and Fig. 1).

5. Conclusions

The primary aims of this review were to synthesize available research involving beef or dual purpose cattle breed behavior comparison studies to discuss how cattle breeds with heritage/traditional/adapted/native/indigenous genetics exhibit foraging behaviors associated with improved adaptation to regional ecosystems and projected climate change effects. In most cases, heritage or adapted cattle types exhibited grazing behaviors more closely associated with adaptive capacity; those behaviors included spending more time walking and traveling, traveling and exploring farther and larger areas of pastures and moving farther distance from water sources, ingesting more diverse suites of flora, and using more rugged terrain.

Our findings suggest that heritage or hybrid cattle breeds with a history of grazing adaptation in a particular locale are more likely to meet adaptation goals than those cattle breeds without. In instances when grazing behavior was compared between breeds derived from the same region (e.g., heritage British vs conventional British), fewer differences were detected. Our review suggests that heritage, hybrid, and otherwise locally derived breeds, display grazing behaviors that demonstrate adaptation to their respective native environments and may help producers meet production goals in similar environments. Further, we conclude that breeds with more natural selection and lower maintenance requirements tend to exhibit less rigid grazing behaviors, which is a necessary coping strategy in variable climates and locales with heterogeneous forage availability, both of which are increasingly common phenomenon caused by climate change.

These findings reaffirm the broader challenge of matching beef cattle breeds to the environment for desired outcomes in a changing climate. Native cattle do not exist in all biomes and the pace of climate change is causing unpredictable ecological patterns at the global scale. Another related issue is the rapidity of loss of heritage breeds, thus researchers and producers are rushing against the clock to mitigate the loss of genetic resources in the midst of a quickly changing climate. Researchers seeking to identify cattle breeds best suited to a given eco-climato-geographic regime should consider the biome of origin of a particular breed as well as key aspects of the breed's genetics and morpho-physiology in addition to the conditions where the breed will be assessed. Additional interdisciplinary research is needed to develop breeding programs that balance the adaptability and sustainability traits displayed by heritage breeds with the growth, feed efficiency and carcass and meat quality traits that producers demand from seedstock to meet the needs of the global beef cattle industry, particularly in developed nations where conventional breeds are considered the norm.

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Footnote

Mention of a trade name, proprietary product or vendor does not constitute a warranty of the product by the USDA or imply its approval to the exclusion of other products or vendors that may also be suitable.

CRediT authorship contribution statement

Matthew M. McIntosh: Conceptualization, Data curation, Formal analysis, Visualization, Writing – original draft, preparation, Writing – review & editing. **Sheri A. Spiegal:** Conceptualization, Data curation, Formal analysis, Visualization, Writing – original draft, preparation, Writing – review & editing, Funding acquisition. **Stacia Z. McIntosh:** Conceptualization, Visualization, Writing – original draft, preparation, Writing – review & editing. **José Castaño Sanchez:** Data curation, Writing – original draft, preparation, Writing – review & editing. **Richard E. Estell:** Writing – review & editing. **Caitriana M. Steele:** Writing – review & editing. **Emile H. Elias:** Writing – review & editing. **Derek W. Bailey:** Writing – review & editing. **Joel R. Brown:** Writing – review & editing. **Andrés F. Cibils:** Conceptualization, Visualization, Writing – review & editing, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data used in this review was retrieved from previously published research

Appendix

A. *Location of studies*

Breed comparison studies in developing nations often focus on production trait comparisons (e.g., fertility in cows and heifers, weight gains in calves and steers, meat quality and yield). In developed nations, conservation issues are often at the forefront of research endeavors, therefore such studies would be more likely to focus on grazing behavior because of its impacts on grazing habitats. Likewise, since most heritage breeds are located in developing nations, there is a lesser chance that those native breeds would be compared against non-native breeds to determine degree of grazing adaptation. This scenario occurred in several studies, however, and points to the pressures to crossbreed or adopt conventional types in places where native genetics may be perceived as less efficient.

In Brazil, the majority of the beef industry is dominated by *indicus* cattle, which are presumably already well-matched to that equatorial eco-climate and which are regarded as conventional types there (Ferraz and Felício, 2010). Similarly, in Australia, a majority of the industry, particularly in the hot arid north, is dominated by *indicus* pure or composite breeds, which producers transitioned to, away from British conventional types like Herefords, in the 1970s; this shift in favor of adapted breeds led to improved animal health and industry gains across the country (Ash et al., 2015). A majority of China's beef industry is already reliant on Chinese native breeds, which are locally adapted across a north – south gradient, wherein breeds from the north have more taurine influence and those from the south have more indicine influence. However, conventional beef sires are often used in terminal breeding programs to improve carcass scores and weight gains of Chinese beef breeds (Li et al., 2013; Sun et al., 2008). The reliance and acceptance of adapted or native breeds in these major beef production countries might explain a relative lack of research from those realms.

B. *Adapted traits*

B.1.

These findings strongly imply that heritage or other autochthonous beef cattle biotypes behave in ways that are more sustainable than conventional types. These findings support our conceptual model by detailing instances where adapted cattle (heritage and local breed categories) exhibited more plastic foraging behaviors (e.g., even grazing distribution and wider diet breadth) in variable and low quality environments compared to conventional types. These qualities match adaptation goals seeking to preserve critical vegetation and those seeking to improve beef production in places where climate change is negatively affecting forage amount and quality (Fig. 5).

B.2.

Nyamuryekung'e et al., (2020) reported differing mothering styles between heritage Raramuri Criollo and Angus × Hereford cows in the Chihuahuan Desert. Criollo tended to exhibit a 'follower' mothering style where the calf maintained a closer proximity to its' dam compared to Angus × Hereford cows which were termed 'hiders,' because cows often left their calves and repeatedly returned to their calf for nursing. The ability to keep the calf nearby likely facilitates travel to areas far from water. These adaptations are thought to result from more natural selection and lower body size maintenance requirements, which affect how heritage Highland or Criollo cows can adjust their grazing behaviors to minimize landscape impacts (Fig. 5).

B.3.

As in the case of Nyamuryekung'e et al., (2020) these authors [Stricklin et al. (1976)] reported that cows of both pure and crossbred Angus backgrounds were spatially constrained because they exhibited a 'hider' or 'alloparental' care style, wherein herd mates took turns serving as "baby sitters," while others spent time foraging (Stricklin et al., 1976). However, Rook et al. (2004) suggested that differences among livestock breeds may be the result of differences in body size and the learning, cultural and social factors associated with rearing systems. Evaluations of breed categories must consider the effects of rearing system and the underlying mechanisms associated with measured traits. For instance, a Scottish study that compared three breeds derived from similar systems (Angus × Limousin, Luing, and Charolais) on relatively large Scottish semi natural hill grasslands, but which did not appear in our literature search, also reported few breed-based foraging behavior differences, which the authors note was inconsistent with the literature (Ricci et al., 2014). In this case, smaller heritage Luing cattle produced less methane than their counterparts did, which was related to their lower energy requirements. This example may be indicative of a body size and backgrounding interaction, wherein, although heritage Luing cows traveled shorter distances from water, their total energy requirements were less resulting in lower methane emissions, and possibly demonstrating a lower environmental footprint in-spite of differences in travel. Although more study would be necessary, these results also reflect those in our meta-analysis (Fig. 3) and conceptual model (Fig. 4), wherein animals with more plastic grazing tendencies (e.g., Criollo) constrained their travel in summer, the same season that Ricci et al. (2014) conducted their trials, when forage resources were richest.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jaridenv.2022.104905.

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